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Community unity: Experimental evidence for meiofauna and macrofauna

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ABSTRACT

The response of two different size classes of marine benthos, macrofauna and meiofauna, to manipulation of disturbance/predation and size specific utilization of biogenic structural refuges by each benthic size category were studied in an intertidal sandflat in Virginia. A field investigation was conducted during August and September 1980 in the same *Diopatra* tube system which Woodin (1978; 1981) previously utilized for macrofaunal experiments. Predator/disturber exclusion cages were employed to experimentally evaluate changes in patterns of abundance of both meiofauna and macrofauna in areas of varying *Diopatra* tube densities (0, 1, 3 or 6 *Diopatra* 0.01 m^{-2}). Samples were collected for macrofauna and meiofauna in areas immediately adjacent to tubes (= inner) and in outer areas with no tubes present from all treatment (caged or uncaged) and tube density (0, 1, 3, 6) combinations after 2 and 4 weeks. A significant increase in total macrofaunal polychaetes, nematodes and copepods was recorded inside cages after 2 and 4 weeks. Those species which were numerically abundant in control sites were also dominant inside cages. Adult densities of the bivalve, *Gemma gemma* increased inside cages after 2 weeks but declined dramatically after 4 weeks. Juvenile *Gemma* abundances, unlike those of the adults, increased inside enclosures after both 2 and 4 weeks. Along with the density increases noted in cages, a variety of main effects (*i.e.,* tube number or position) and interactions were revealed, but these were not consistent even among benthos of similar sizes. Although densities of both meiofauna and selected macrofauna increased over similar time scales in response to predator/disturber exclusion, their spatial patterns and relationships with tubes were highly variable. Our analyses of spatial patterns of macrofauna and meiofauna in caged and uncaged sites do not fit our *a priori* predictions necessary to support a refuge hypothesis for all meiofauna and macrofauna by *Diopatra* tubes. The discrepancies between the findings of this study and earlier reports of macrofaunal utilization of *Diopatra* tube-caps as refuges may be related to yearly changes in community composition and/or predator/disturber activity or possibly the time scale of experiments reported here. We suggest that simultaneous monitoring of various size classes from soft-bottom communities, coupled with field experimentation, would provide valuable insight into the relative importance of forces organizing soft-bottom assemblages.

1. Introduction

Catastrophies and other less dramatic physical disturbances have long been recognized as important in determining the distributions and abundances of organisms

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(Andrewartha and Birch, 1954). Much is also known about how episodes of biological disturbance influence the establishment, maintenance, and turnover of biotic assemblages (e.g., terrestrial habitats: Richards and Williamson, 1975; Platt, 1975; Connell, 1978; aquatic habitats: Orth, 1977; Sousa, 1979, 1980; Paine, 1979; Paine and Levin, 1981; Woodin, 1978, 1981; Suchanek, 1981).

In almost all marine investigations of disturbance the organisms of interest have been confined to a particular taxon or size class. This is especially true in soft-bottom systems where researchers have focused on either macrofauna, organisms retained on an 0.5 mm or larger sieve (e.g., McCall, 1977; Woodin, 1978) or meiofauna, organisms retained on an 0.063 mm sieve but passing through a 0.5 mm sieve (e.g., Bell, 1980; Thistle, 1980; Sherman and Coull, 1980; Reidenauer and Thistle, 1981). Such traditional approaches preclude detailed evaluation of differential responses of size classes to disturbance events (but see Rhoads *et al.,* 1978; Brenchley, 1981; Wilson, 1981). However we know that organisms escape in size (e.g., Dayton, 1971; Reise, 1977; Brenchley, 1981; Suchanek, 1981) and that recovery times of meiofauna after disturbance may be much shorter than those of macrofauna (see Bell and Devlin, 1983 and above references for comparisons). In marine sedimentary systems these size-related differences are a function of a host of factors including (1) the mode of disturbance; (2) the frequency of disturbance; (3) the generation time of organisms being disturbed; (4) the mechanisms and rates of immigration of new colonizers; and (5) the availability of refuges from disturbances. Present information indicates that generation times of meiofauna are shorter than those of macrofauna organisms (e.g., Gerlach, 1971, for meiofauna; Sellmer, 1967 for macrofauna) and the meiofauna may recolonize sediments via sediments or resuspension (e.g., Bell and Coen, 1982). Juvenile macrofauna (which may be considered "temporary meiofauna") may also move through sediments, and via resuspension (Sellmer, 1967) while adult macrofauna may have more restricted movement via the water column (however, see Dauer *et al.,* 1980). Thus, what appears to be a "disturbance" to one benthic size category may have little impact, or only one of very short duration, on the community structure of another. By analogy, those physical or biological structures which serve as refuges from disturbance (e.g., Menge and Lubchenco, 1982) for one size class of organism may be ineffective for others (see Woodin (1978) for further discussion).

One method for discerning size class related responses to disturbance events is to monitor all biotic components of a benthic assemblage but this approach is logistically unfeasible on any extensive basis. Alternatively, investigations on subsets of organisms spanning more than one category or size range represent an improvement to the above dilemma by investigating relationships between at least two different size scales. The following study summarizes an investigation of the response of two different size classes, macrofauna and meiofauna, to manipulation of disturbance agents and size-specific utilization of biogenic structural refuges. The goal of our study was to evaluate "community unity" [*sensu* Buzas (1978)] of a soft-bottom assemblage by

examining whether the responses of different size classes of a sedimentary community coincided temporally and spatially. Specifically, information gathered from this study was examined to test: (1) whether disturbance selectively influences the density of different size classes of benthic organisms; (2) whether different size classes respond to exclusion of disturbance agents on the same time scale; (3) whether structural refuges previously reported for macrofauna (Woodin, 1978; 1981) are similarly utilized by meiofauna; and (4) whether patterns of response by meiofauna to reduction of disturbance closely parallel or complement the responses of macrofauna.

2. Materials and methods

a. Background information. We used the results of previous studies conducted by Woodin (1978; 1981) on macrofauna and tube structures of the polychaete, *Diopatra cuprea,* as the basis for our disturbance study. Woodin (1978, 1981) indicated that (1) densities of infaunal polychaetes were naturally higher in the vicinity of dense (6×0.01 m^{-2}) *Diopatra* tubes than elsewhere; (2) the association between tubes and macroinfauna was due to the physical presence of tube structure (Woodin, 1978); and (3) when cages which excluded large epibenthic organisms ("disturbers") were placed over areas with either 0 or 6 tubes $\times$ 0.01 m^{-2}, numbers of individuals of macroinfauna repeatedly increased inside cages in three separate trials in three consecutive years [see Woodin (1981)]. Woodin (1978; 1981) thereby concluded that high densities (6×0.01 m^{-2}) of the large tubes of *Diopatra* naturally impeded activities of predators/disturbers and thus provided refuges for macrofauna. Note, however, that the refuge is imperfect because increases in macrofaunal density are still found inside cages with 6 tubes [see Young *et al.* (1976) and Blundon and Kennedy (1982) for an analogous situation]. Some of the increases charted inside of cages and around high densities of polychaete tube structures may have been related to "larval accumulation" or trapping of larval forms around tube structures and not relaxation of predator effects [Fig. 4 in Woodin (1981), results in (1978)]. However in most of the experiments the data did not strongly support the "larval accumulation" hypothesis [Fig. 2 in Woodin (1981), results in (1974) and (1978)] but rather supported the "refuge" hypothesis.

Given the above, we conducted a set of short-term field experiments to evaluate both meiofaunal and macrofaunal response to exclusion of disturbance agents. Because (1) many studies have emphasized that short-term sampling is necessary to monitor many experimentally induced responses of infaunal organisms (e.g., Thistle, 1980; Bell and Devlin, 1983; Van Blaricom, 1982) and (2) any study incorporating both meiofaunal and macrofaunal sampling faces severe logistical (time) demands, we chose to conduct a short-term, yet comprehensive, experiment. Extensive experimental and descriptive information on the relationship between macrofauna, tube structure and disturbance agents exists which demonstrates predator/disturbance by epibenthic forms (e.g., *Limulus polyphemus* and *Callinectes sapidus*) on infaunal organisms in upper

sediment layers (e.g., Sellmer, 1967; Green and Hobson, 1970; Woodin, 1981). Our information on meiofauna and disturbance (disturbance of upper sediment layers rather than predation is probably more germane here) agents is somewhat limited. We conducted preliminary samplings in Spring 1980 to evaluate potential utilization of *Diopatra* tubes by meiofauna and found that copepod density, like that of macroinfauna (Woodin, 1981), was significantly higher in areas of 6 × 0.01 m^{-2} *Diopatra* tubes compared to areas with 0 tubes × 0.01 m^{-2} (Bell, unpublished data). We did not assess the direct impact of disturbance agents on meiofauna in the field, although this has been repeatedly demonstrated for surface dwelling meiofauna in other areas (Sherman and Coull, 1980; Reidenauer and Thistle, 1981; Sherman *et al.*, 1983).

b. Study site. We conducted our study in Tom's Cove, Virginia on the same intertidal (−0.1 m) sandflat utilized previously by Woodin (1978; 1981). We selected this site for a number of reasons. We had extensive background on macrofaunal assemblages and larval recruitment into the area. Additionally, juveniles of the bivalve, *Gemma gemma,* were seasonally abundant at this site and could be sampled adequately with meiofaunal-sized cores. The *Diopatra* tube system is expansive, easily accessible at low tide and relatively protected from human interference. Disturbance agents (blue crabs, rays, horseshoe crabs) are abundant and their feeding/disturbance activities are readily observable in the shallow water areas. Sediment grain size is approximately 0.5 mm with little silt-clay to produce problematic accumulations inside experimental cage treatments (Virnstein, 1978). Additional details of the study site are available in Woodin (1981).

c. Experimental design. We followed the experimental approach previously utilized by Woodin (1981). We used predator/disturber exclusion cages to experimentally evaluate changes in both meiofaunal and macrofaunal patterns of abundance produced by this manipulation in areas of varying *Diopatra* tube densities. Complete cages were constructed of plastic mesh with 0.62 cm openings and enclosed an area of 0.25 m^2 × 20 cm high extending 5.0 cm below the sediment and 15.0 cm above the sediment. Corners of the cages were attached with nylon line to 50 cm × .25 cm dowels hammered 40 cm into the sediments. We established a transect at −0.1 m parallel to the shore and randomly located cage and staked-out control treatments in a variety of pre-determined *Diopatra* tube densities (0, 1, 3, or 6) within a 600 m^2 area. All control and treatment sites were centered around the predetermined clump of *Diopatra* tubes.

Experiments were initiated on August 3, 1980 and samples were taken 2 and 4 weeks later. We chose this experimental time interval as a compromise between predicted macrofaunal (months, e.g., Woodin, 1981) and meiofaunal (days, weeks; e.g., Bell, 1980; Thistle, 1980, 1981) responses to experimental manipulations. We also chose this time interval because cages which remain in the field for a relatively long period of

time increase their probability of destruction, sediment accumulation or becoming enclosure experiments (see Virnstein, 1978). One benefit of inclusion of the meiofaunal size range and short term sampling in our experiment is that any accumulation of macrofaunal larvae associated with cage or around tube structure can be identified directly. In addition, juvenile decapods declined in abundance during late summer and early fall (Woodin, unpub.) which also decreases the probability of confounding experiments with activities of unwanted organisms [see Reise (1977)]. *Limulus* activity also declines, but is not eliminated, in the fall reducing the risk of cage loss to bulldozing (Woodin, 1981).

The 2-week experiment (initiated 3 August, terminated 17 August, 1980) consisted of complete cages and unmanipulated control areas in sites with 0 and 6 per 0.01 m^{-2} *Diopatra* tubes (hereafter referred to as 0D and 6D). The 4-week experiment (initiated 3 August, terminated 5 September, 1980) included tube densities of 0, 1, 3 and 6 *Diopatra* tubes per 0.01 m^2 (=0D, 1D, 3D, 6D) in complete cages and unmanipulated control sites.

Although caging techniques may be useful tools for researchers, we are cognizant of problems inherent in their utilization (i.e., Virnstein, 1978). We specifically designed our experiment to avoid the pitfalls of caging. Firstly, because our experiments were run over a short time interval, the probability of cages being destroyed, accumulating fine sediments or becoming enclosure experiments was minimized. Secondly, to assess possible cage artifacts, cages without sides (tops only) and cages without tops (sides only) were included in the experimental design. Cage control treatments were constructed with identical dimensions as full cages and erected in areas of 0D only. Our field observations confirmed that partial cages allowed epibenthic macrofauna access to designated areas and thus should provide assessment of the effect of introduced cage structure. Other types of cage controls such as 3-sided cages or cages with holes in them were not selected because one of us (S.A.W.) noticed that some epibenthic forms treated such cage controls as complete cages and other epibenthic forms, notably blue crabs, appeared preferentially to inhabit 3-sided cages. We tried to minimize any reef effect of our cages by daily removal of macroalgae, hermit crabs, *Ilynassa* or birds near, or on, cage structure. Only macroalgae had to be removed regularly; they became entangled with support stakes outside of the cage. All cages, partial and complete, as well as unmanipulated control areas were replicated five times for both the 2-week and 4-week experiments. Each site was sampled on only one date to avoid artifacts associated with repeated sampling. Finally, sampling of all cage and cage control treatments was conducted 17 cm away from cage edges so edge effects of cage structure would be minimized.

d. Field sampling and laboratory procedures. Macrofauna and meiofauna were sampled from experimental treatments during low tide over a 2-day period, 2 and 4 weeks after initiation of experiments. Macrofaunal cores were taken as in Woodin

(1981); i.e., inserting two metal frames (0.01 m^2 × 14 cm deep and 0.02 m^2 × 14 cm deep) into the sediments. The inner 0.01 m^2 frame (= inner sample) enclosed an area with prescribed densities of *Diopatra* tubes (0D, 1D, 3D, or 6D) while the outer frame enclosed the inner frame plus the surrounding 0.01 m^2 area which contained 0D *Diopatra*. One set of inner and outer samples was taken per replicate treatment, 17 cm from cage or control edges. *Diopatra* tube-caps were clipped and removed from the surface before sampling to avoid contamination of samples with fauna from the tube-cap (Brenchley, 1975; Woodin, 1978). Four meiofaunal samples were taken with straw corers (0.6 cm inner diameter, 0.28 cm^2 total area) to a depth of 2.5 cm (the redox layer was approximately 2.1 cm deep) from both the inner and outer macrofaunal cores. Meiofaunal samples were taken in a specified spatial array (for use in another study) from randomly chosen areas within the inner and outer locations. All macrofaunal (total = 160; 2 wk, 60; 4 wk, 100) and meiofaunal (total = 640; 2 wk, 240; 4 wk, 400) samples were fixed in 10% formalin-seawater.

In the laboratory, macrofaunal samples were washed over a 0.5 cm sieve and preserved in a 10% formalin-seawater solution stained with Rose Bengal. Our procedure departs from processing originally utilized by Woodin (1978, 1981) (i.e., a 1.0 mm sieve) but we chose to examine a strict continuum of size classes (meiofauna retained on 0.063 mm sieve mesh but passing 0.5 mm mesh; macrofauna retained on 0.5 mm mesh sieve) in our experiments. Samples were then sorted, enumerated under a dissecting microscope and identified to lowest taxon possible. Any *Diopatra* encountered in samples were excluded from the analysis. Meiofaunal samples were sorted and enumerated under a dissecting microscope and organisms were identified to major taxa. Copepods and juvenile macrofauna were saved for subsequent species identification and/or size class measurement. Any macrofauna (>0.5 mm) recovered from meiofaunal straw samples were added to totals from the appropriate macrofaunal core.

e. Statistical analyses. To examine the question of refuge utilization, we used the information presented by Woodin (1978; 1981) as a basis for analyses of our experimental data although our time scale is shorter. Given the previous findings for macrofaunal response to predator exclusion in different densities of *Diopatra* tubes, we predicted that if the refuge hypothesis were supported by our data the following would be true: (1) macroinfaunal (and meiofaunal) densities would be significantly greater inside complete cages than in unmanipulated sites (exclusion effect: cages versus unmanipulated sites); (2) macroinfauna densities in inner samples from unmanipulated sites would be significantly greater in areas with 6 *Diopatra* tubes than in areas with 1 or 0 *Diopatra* tubes (tube density effect: 6D > 1D = 0D); (3) macroinfaunal densities in inner samples from complete cages would not be significantly greater in areas with 6 *Diopatra* tubes than in areas with 1 or 0 *Diopatra* tubes although, given the imperfections of the 6D refuge, macroinfaunal densities would be greater inside

complete cages than in 6D unmanipulated sites; this lack of a tube effect inside complete cages would be seen as a significant tube density × exclusion interaction; (4) regardless of the number of *Diopatra* tubes present in the inner sample in unmanipulated sites macroinfaunal densities in outer samples would not be significantly greater than those in inner samples from 0 *Diopatra* tube areas (position × tube density effect: outer samples 6D = 1D = 0D); (5) there would be a significant exclusion × tube density × position effect because the position × tube density effect (prediction no. 4) would change as a function of exclusion (complete cages: inner samples = outer samples regardless of tube density: unmanipulated sites: inner samples = outer samples in 0D and 1D sites, inner samples > outer samples in 6D sites). Because Woodin (1978; 1981) did not report results for areas with 3 *Diopatra* tubes, we could not formulate such precise predictions for 3D sites. However, given the refuge hypothesis, we would expect macroinfaunal densities in inner samples from unmanipulated areas with 3 *Diopatra* tubes to be intermediate between densities in 1D and 6D sites (inner samples: 6D > 3D > 1D = 0D). These predictions of course assume that the macrofauna will respond within 2 or 4 weeks. The experiments of Woodin (1981) upon which these predictions are based ran a minimum of 2 months. Given the number of effects that we *a priori* expected to see as significant interaction terms, we conducted a three-way ANOVA on densities of dominant macrofaunal and meiofaunal taxa from our experiments with exclusion (a = 2, unmanipulated and caged), tube density (b = 3 or 4, 0, 1, and 6D or 0, 1, 3, 6D), and position (c = 2, inner and outer samples) as the main effects. Two- and 4-week experiments were analyzed separately for both macrofaunal and meiofaunal taxa and compared to evaluate responses of the different size groups to manipulation of predators/disturbers. These analyses allowed us to test for all goals of our experiments: similarity in time of response, similarity in response to exclusion of predators and similarity in refuge utilization. We analyzed our data at the major taxon level and the species level for polychaetes, bivalves and meiofaunal copepods. Dominant macrofauna and meiofauna taxa were defined as those whose mean abundances in our samples exceeded 5 individuals in at least one treatment.

Log $(Y + 1)$ transformed meiofaunal and macrofaunal data were utilized because equality of variances of nontransformed data was rejected by the Burr-Foster Q test ($P > 0.05$). Those main effects which were identified as significant at $P \leq 0.05$ in the ANOVA were then analyzed with a multiple comparison test, a least significant difference procedure [Fisher significant difference ($\alpha = 0.05$); Carmer and Swanson (1973)]. Because the meiofaunal core samples were not taken randomly within each replicate exclusion treatment the mean of the four subsamples from the spatial array was used in the ANOVA.

Data from the cage controls (tops only and sides only, in 0D areas) were compared to cage and control treatments in a two-way ANOVA with position and treatment as main effects. If significant main effects were noted ($P \leq 0.05$), the Fisher significant difference procedure was used to locate significant differences among the means. For

sake of brevity, only significant main effects and interactions from cage, control and cage control treatments are reported below.

3. Results

a. Macrofauna: control site. Gemma gemma, a small bivalve which lives just below the sediment surface, was the most abundant macrofaunal organism in 1980 as was true in 1974, 1975 and 1976 (Woodin, 1978; 1981). Size class analyses of *G. gemma* collected from meiofaunal straw cores as well as a comparison of *G. gemma* densities in macrofaunal and meiofaunal samples indicated that 79% of the *G. gemma* population was in the meiofaunal size range (Bell, unpublished). This high percentage of small-sized individuals has been reported elsewhere (e.g., Nichols, 1976). The differences between *G. gemma* abundance reported in this study and those of Woodin (1978; 1981) (see Table 1) do not appear to be related to sieve size, however. A comparison of *G. gemma* individuals in the >0.5 mm size range from Woodin's earlier study (Woodin, unpublished) with those in the >0.5 mm size range reported here indicates that *G. gemma* densities were still an order of magnitude higher in our 1980 samples.

Polychaetes were the second most abundant macrofaunal taxon. Densities in 1980 were similar to those reported by Woodin (1978; 1981) (Table 1) but the species composition was markedly different (Table 2). This is not surprising given that the assemblage described by Woodin varied in species composition during the three years of study (1974–1976, Table 2). *Streblospio* was consistently abundant as during this study (1980, Table 2).

In all months except August 1974, Woodin (1978) documented significantly greater polychaete abundances in areas with 6D than in areas with 0 or 1D (Table 1). This pattern of increased abundances was quite localized and did not extend much beyond the clump of *Diopatra* tubes (inner vs. outer samples, Woodin, 1978). In the study reported here we observed a similar pattern. Total polychaete abundances were significantly greater in inner samples from areas with 6D than from areas with 0D (one way ANOVA 15 August: $F = 8.4$, $P \leq 0.05$; 5 September: $F = 26.5$, $.01 \leq P < .05$, Tables 1, 3, and 5) while outer samples from areas with 0 or 6D were not significantly different in polychaete densities (Tables 4 and 6). Woodin did not find *Gemma gemma* densities to be consistently higher in 6D areas (Woodin, 1978) nor did we in this study (Table 1). Thus, as Woodin (1978) originally described, the pattern of increased abundances around *Diopatra* tubes, which Woodin ascribed to a "refuge" effect of the tubes, was apparent in control samples for total polychaetes but not *G. gemma* (Table 1).

b. Meiofauna: control sites. Nematodes, copepods and juveniles of the bivalve, *Gemma gemma,* were the dominant meiofauna found in our sites. All meiofauna were restricted to the top 1–2 cm of sediment above the redox layer. An unidentified ostracod species was also common. Other meiofaunal taxa (i.e., the tardigrade

Table 1. Comparison of densities [means and standard deviations (in parentheses)] of macrofauna in inner samples (0.01 m^2 × 14 cm) from control sites in Tom's Cove, Virginia. Data from 1974–1976 are from Woodin (1978) and (1981); data from 1980 are this study. 0D, 1D, 6D refer to densities of *Diopatra* tubes in inner samples. nd = no data.

	Polychaetes			*Gemma*		
	0D	1D	6D	0D	1D	6D
1974						
July	23.5(5.5)	22.7(11.9)	54.3(0.6)	38.7(17.6)	37.7(7.6)	36.7(18.8)
August	17.3(4.0)	11.0(4.4)	15.3(0.6)	44.7(5.1)	46.3(6.7)	43.3(10.6)
October	19.0(3.0)	23.3(0.6)	44.3(12.6)	8.7(5.0)	8.0(6.1)	15.0(6.6)
1975						
August	13.4(7.4)	nd	23.6(10.4)	58.0(36.2)	nd	67.8(21.7)
September	14.2(6.4)	nd	nd	16.4(7.7)	nd	nd
October	12.0(2.2)	nd	nd	9.4(7.7)	nd	nd
1976						
July	31.5(5.4)	nd	nd	14.8(8.3)	nd	nd
October	17.7(7.3)	nd	nd	8.5(7.2)	nd	nd
1980						
August	5.0(4.1)	nd	24.4(1.9)	425(121)	nd	360(58)
September	12.5(6.2)	16.2(5.3)	30.4(9.0)	686(416)	722(214)	709(264)

Batillipes muris and juvenile polychaetes) are seasonally abundant (Bell, unpublished) but were found only in low densities in August and September, 1980. Four harpacticoid copepod species—*Leptastacus* sp., *Zausodes arenicolus,* Diosaccid sp., and *Paralaophonte* sp.—and a cyclopoid copepod composed over 90% (by number) of the copepod assemblage. No life history information is available on these copepods species but *Leptastacus* sp. and *Zausodes arenicolus* are common in sands along the

Table 2. Numerically dominant polychaete species in inner samples (0.01 m^2 × 14 cm) with 0 or 6 *Diopatra* tubes. Data for 1974, 1975, and 1976 from Woodin (1978, 1981 and unpublished). Mean densities given in parentheses. (nd = no data).

Date	0D	6D
1974 August	*Spiochaetopterus oculatus* (7.7) *Streblospio benedicti* (6.3)	*Spiochaetopterus oculatus* (3.7) *Streblospio benedicti* (3.0) *Nereis acuminea* (3.0)
1975 August	*Streblospio benedicti* (5.6) *Heteromastus filiformis* (2.8)	*Streblospio benedicti* (5.4) *Nereis acuminea* (4.6)
1976 July	*Tharyx acutus* (14.0) *Streblospio benedicti* (3.8)	nd
1980 August	*Streblospio benedicti* (2.2)	*Polydora ligni* (14.9) *Heteromastus filiformis* (2.2)
1980 September	*Streblospio benedicti* (6.2)	*Polydora ligni* (7.2) *Nereis succinea* (5.0) *Heteromastus filiformis* (4.0)

Table 3. Inner samples (2 weeks). Means and standard deviations (in parentheses) for numbers of dominant macroinfauna and meiofauna in inner samples from sites with 0 or 6 *Diopatra* tubes on 15 August 1980. Only species with a mean density of 5 or more are listed individually. $N = 5$. Macrofauna: mean densities in 0.01 $m^2 \times 14$ cm samples. Meiofauna: mean densities in 0.28 $cm^2 \times 2.5$ cm samples.

	Unmanipulated Sites		Complete Cages	
	0D	6D	0D	6D
A. Macrofauna				
1. *Gemma gemma*	425(121)	360(58)	287(113)	713(353)
2. Total polychaetes	5.0(4.1)	24.4(19.1)	38.0(25.0)	104.2(62.4)
a) *Polydora ligni*	0.5(0.5)	14.8(14.6)	7.2(6.6)	62.4(53.4)
b) *Streblospio benedicti*	2.2(2.9)	0.6(0.8)	18.4(12.0)	6.4(3.0)
3. Total macroinfauna	437(123)	406(69)	325(113)	817(398)
B. Meiofauna				
1. Juvenile *Gemma gemma*	4.2(1.2)	6.0(1.1)	12.9(9.7)	17.1(9.0)
2. Nematodes	17.5(4.5)	36.1(4.2)	29.1(17.9)	41.8(9.3)
3. Total copepods	9.8(4.7)	10.8(2.5)	7.3(4.5)	30.9(5.9)
a) *Leptastacus* sp.	3.0(1.0)	4.0(1.3)	3.4(2.2)	18.9(7.9)
4. Ostracods	2.9(2.1)	2.7(2.1)	5.4(3.1)	6.5(3.8)
5. Total meiofauna	39.1(9.4)	57.0(46.7)	62.5(31.6)	100.3(21.4)

east coast of North America and the latter is common in sands from the west coast of Florida (Kern *et al.*, 1984; Reidenauer and Thistle, 1981). *Paralaphonte* is thought to be an epibenthic form.

During August and September 1980 we did not find any major meiofaunal taxon that exhibited significant localized patterns of greater abundance around 6D com-

Table 4. Outer samples (2 weeks). Means and standard deviations (in parentheses) for numbers of dominant macroinfauna and meiofauna in outer samples from sites with 0 or 6 *Diopatra* tubes on 15 August 1980. Only species with a mean density of 5 or more are listed individually. $N = 5$. Macrofauna: mean densities in 0.01 $m^2 \times 14$ cm samples. Meiofauna: mean densities in 0.28 $cm^2 \times 2.5$ cm samples.

	Unmanipulated Sites		Complete Cages	
	0D	6D	0D	6D
A. Macrofauna				
1. *Gemma gemma*	600(115)	412(42)	353(94)	533(259)
2. Total polychaetes	4.0(1.2)	3.8(2.5)	27.0(15.3)	19.0(11.6)
a) *Streblospio benedicti*	0.2(0.4)	0.2(0.4)	8.5(5.4)	5.0(2.5)
3. Total macroinfauna	605(116)	429(50)	405(98)	563(256)
B. Meiofauna				
1. Juvenile *Gemma gemma*	6.3(5.2)	4.8(1.5)	11.2(6.3)	8.4(4.8)
2. Nematodes	25.3(17.9)	16.4(2.4)	29.5(18.0)	37.9(15.0)
3. Total copepods	7.8(4.6)	6.5(3.5)	12.3(4.0)	21.6(12.8)
a) *Leptastacus* sp.	3.9(3.2)	3.0(1.9)	7.9(3.5)	21.5(9.6)
4. Ostracods	2.9(1.5)	2.0(1.4)	5.6(2.1)	8.7(6.4)
5. Total meiofauna	35.8(23.8)	32.5(8.6)	61.6(21.5)	81.2(30.0)

Table 5. Inner samples (4 weeks). Means and standard deviations (in parentheses) for numbers of dominant macroinfauna and meiofauna in inner samples from sites 0, 1, 3, or 6 *Diopatra* tubes on 5 September 1980. Only species with a mean density of 5 or more are listed individually. $N = 5$. Macrofauna: mean densities in $0.01 m^2 \times 14$ cm samples. Meiofauna: mean densities in $0.28 cm^2 \times 2.5$ cm samples.

	Unmanipulated Sites				Complete Cages			
	0D	1D	3D	6D	0D	1D	3D	6D
A. Macrofauna								
1. *Gemma gemma*	686	722	831	709	100	92.0	169	275
	(416)	(214)	(643)	(264)	(55.0)	(61.0)	(79)	(150)
2. Total polychaetes	12.5	16.2	17.4	30.4	59.0	46.0	59.0	25.0
	(62.0)	(5.3)	(9.0)	(9.0)	(55.0)	(30.0)	(48.0)	(20.0)
a. *Streblospio benedicti*	6.2	2.0	2.0	1.4	27.0	17.5	15.0	6.6
	(2.9)	(1.5)	(3.3)	(1.1)	(25.0)	(10.2)	(16.0)	(7.8)
b. *Heteromastus filiformis*	0.2	1.2	2.0	4.0	27.0	10.0	27.0	4.0
	(0.5)	(1.6)	(0.7)	(2.2)	(30.0)	(10.0)	(25.0)	(5.0)
c. *Paraonis* sp.	1.2	4.2	0.4	3.0	9.0	6.0	4.8	0.6
	(1.8)	(5.1)	(0.5)	(5.6)	(8.7)	(10.7)	(5.6)	(1.3)
3. Total Macrofauna	769	738	870	792	161	138	228	301
	(443)	(217)	(672)	(270)	(85)	(42)	(103)	(152)
B. Meiofauna								
1. Juvenile *Gemma gemma*	5.2	8.0	9.4	6.1	7.7	8.4	14.4	17.4
	(1.6)	(2.0)	(5.0)	(2.3)	(4.4)	(3.9)	(8.1)	(5.6)
2. Nematodes	25.5	16.5	12.7	8.2	31.7	36.6	21.2	35.7
	(13.2)	(14.0)	(3.0)	(3.4)	(1.3)	(19.3)	(3.1)	(8.2)
3. Total Copepods	7.0	9.3	10.5	6.7	20.7	30.0	25.1	44.7
	(3.4)	(1.2)	(4.1)	(2.6)	(9.1)	(9.9)	(14.4)	(9.5)
a. *Leptastacus* sp.	3.4	5.3	4.6	3.9	10.5	16.6	16.9	31.1
	(2.0)	(1.6)	(1.5)	(1.8)	(6.3)	(8.5)	(9.1)	(7.5)
b. *Zausodes arenicolus*	2.1	0.5	0.7	1.1	2.2	6.2	5.0	5.2
	(2.1)	(0.8)	(0.5)	(0.8)	(1.4)	(1.4)	(5.4)	(4.0)
c. Nauplii	0.8	0.4	1.5	1.3	2.1	3.7	2.9	6.1
	(0.7)	(1.4)	(1.4)	(1.6)	(0.9)	(2.7)	(3.4)	(4.7)
4. Ostracods	1.5	1.8	3.2	2.4	5.7	6.4	7.7	8.5
	(0.9)	(0.7)	(1.0)	(1.8)	(3.2)	(6.0)	(5.8)	(4.7)
5. Total Meiofauna	40.7	37.0	33.0	25.5	63.8	87.1	82.4	116.2
	(15.2)	(12.5)	(11.1)	(9.1)	(22.1)	(26.6)	(32.6)	(22.4)

pared to 0D (Tables 3 and 5; one way ANOVA, $P > 0.05$) in contrast to our findings for macrofaunal polychaetes at these times (see above) and meiofaunal copepods in April samples [total copepods ($\bar{x} \pm$ S.D.): 0D: 7.1 (± 3.2), 6D: 15.3 (± 6.5)]. Densities of meiofaunal taxa were not significantly different in outer areas with 0D or 6D (Tables 4 and 6). Therefore patterns of meiofaunal abundance in August and September 1980 did not correspond to those predicted for a "refuge" effect; i.e., densities from inner samples with 6D were not significantly greater than those from 0D sites.

Table 6. Outer samples (4 weeks). Means and standard deviations (in parentheses) for numbers of dominant macroinfauna and meiofauna in outer samples from sites 0, 1, 3, or 6 *Diopatra* tubes on 5 September 1980. Only species with a mean density of 5 or more are listed individually. $N = 5$. Macrofauna: mean densities in 0.01 $m^2 \times 14$ cm samples. Meiofauna: mean densities in 0.28 $cm^2 \times 2.5$ cm samples.

	Unmanipulated Sites				Complete Cages			
	0D	1D	3D	6D	0D	1D	3D	6D
A. Macrofauna								
1. *Gemma gemma*	640	550	644	638	138	161	373	298
	(212)	(149)	(290)	(317)	(57)	(256)	(253)	(276)
2. Total polychaetes	13.2	10.8	9.4	15.2	116	106	72.0	68.0
	(2.2)	(4.2)	(8.0)	(9.0)	(74)	(56)	(45.0)	(32.0)
a. *Polydora ligni*	0.6	0.6	0.2	5.2	1.5	4.2	1.0	6.6
	(0.6)	(0.8)	(0.4)	(7.9)	(1.6)	(5.0)	(1.2)	(7.3)
b. *Streblospio benedicti*	5.4	3.6	2.6	3.0	59.0	34.0	45.0	34.0
	(3.2)	(1.9)	(3.7)	(2.8)	(26)	(24.8)	(18.0)	(22.0)
c. *Heteromastus filiformis*	0.8	2.4	1.2	0	33.0	18.0	17.0	8.0
	(1.3)	(2.3)	(2.1)		(37.0)	(24.0)	(30.0)	(9.0)
3. Total Macroinfauna	655	558	654	653	245	267	446	368
	(212)	(150)	(292)	(325)	(46)	(298)	(264)	(262)
B. Meiofauna								
1. Juvenile *Gemma gemma*	4.4	4.0	5.3	8.3	9.5	8.1	7.4	8.0
	(1.2)	(0.5)	(1.2)	(6.6)	(4.4)	(4.5)	(1.4)	(3.4)
2. Nematodes	15.7	10.6	13.4	8.7	22.0	21.9	16.4	26.5
	(6.2)	(4.4)	(3.0)	(7.1)	(7.0)	(13.9)	(3.6)	(13.8)
3. Total Copepods	7.0	5.3	6.7	7.7	12.9	12.1	12.1	15.0
	(3.4)	(1.6)	(3.0)	(8.8)	(6.2)	(7.2)	(3.9)	(6.5)
a. *Leptastacus* sp.	4.7	2.9	3.1	3.9	5.9	6.6	7.2	8.6
	(2.9)	(1.7)	(1.4)	(3.5)	(4.2)	(6.1)	(2.6)	(6.0)
4. Ostracods	2.8	1.2	1.2	4.2	5.7	6.6	6.4	9.9
	(1.1)	(0.7)	(1.0)	(4.1)	(4.0)	(2.5)	(3.1)	(3.9)
5. Total meiofauna	32.4	20.3	28.3	31.0	56.4	62.4	46.4	67.2
	(8.3)	(5.4)	(1.8)	(26.9)	(15.3)	(31.6)	(7.4)	(22.5)

c. Macrofauna and meiofauna: cage controls. We examined cage control treatments to verify that responses to predator/disturber exclusion were not a result of cage artifacts. As shown in Table 7 densities in unmanipulated sites (0D) were not statistically different from densities in sides only or tops only cage controls over the time scale of our experiment for polychaetes, *Gemma gemma,* nematodes or copepods. The magnitude of difference between complete cages and cage controls is large for polychaete and copepod abundances. If cage structure did impose an artifact we would have expected to see increases in densities inside sides-only cage controls for all taxa compared to areas with no cages. There is no evidence for such a pattern within our data set for any taxon except juvenile *G. gemma* after 4 weeks (Table 7). Juveniles of

Table 7. Cage Controls from 2- and 4-week experiments from 0D sites for I. macrofaunal and II. meiofaunal taxa. Summary of 2-way ANOVA on dominant taxa from cages, unmanipulated sites and cage controls (sides only; tops only) and Fisher significant difference tests on significant sources of variation in ANOVA. Means (in parentheses) are given below treatments. Means that are not statistically different are underlined by a common line. Ca = complete cage; S = sides only; T = tops only; U = unmanipulated site (*$P < 0.05$; **$P \leq 0.01$; ***$P \leq 0.005$; ****$P \leq 0.001$) ($N = 5$). There were no position or treatment × position effects for any taxa at two or four weeks.

	F statistic	Multiple comparison
I. Macrofauna		
A. Two Weeks		
1. Total Polychaetes exclusion	8.0***	Ca S U T (65.0) (23.0)(9.0)(9.0)
B. Four Weeks		
1. *Gemma* exclusion	23.9****	U T S Ca (1326)(1157)(868) (238)
2. Total Polychaetes exclusion	8.9****	Ca S T U (175) (46.0)(22.0)(20.0)
II. Meiofauna		
A. Two Weeks		
1. Nematodes exclusion	8.5****	Ca U S T (58.6) (42.8)(40.2)(38.0)
2. Juvenile *Gemma* exclusion	3.8*	Ca U S T (24.1) (10.5)(9.4)(6.7)
B. Four Weeks		
1. Nematodes exclusion	5.5**	Ca U S T (53.7) (41.2)(37.2)(35.0)
2. Total Copepods exclusion	7.1***	Ca U T S (33.6) (14.0)(12.0)(7.8)
3. Juvenile *Gemma* exclusion	11.7****	S Ca U T (17.7)(17.2) (9.6)(4.7)

G. gemma increased in abundance inside sides-only cage controls compared to unmanipulated sites but this was found only in the 4-week experiment (Table 7).

d. Macrofauna and meiofauna: 2-week experiment. The densities of macrofauna and meiofauna from 0D and 6D control and cage treatments were examined to compare responses of both size classes to manipulation and to test our predictions about responses consistent with the refuge hypothesis (see Materials and Methods).

Statistical analyses of results from caging experiments in August 1980 (2 weeks) are presented in Table 8 for macrofauna. Given the absence of a significant relationship between the densities of *Gemma gemma* and the densities of *Diopatra* tubes in unmanipulated sites (Tables 1, 3, and 4) we did not expect to see a pattern related to

Table 8. ANOVA on I. macrofaunal and II. meiofaunal taxa from Tables 3 and 4 from 2 week experiment. Means (in parentheses) are given below treatments. For those main effects which are identified as significant the direction of significant difference is indicated. For those interactions which were identified as significant the order of means (highest to lowest) is presented (no test of significance among interaction terms is possible). Ca = complete cage; U = unmanipulated sites; In = inner; Ou = outer; 0, 6 = tube number. Other abbreviations as in Table 7.

	I. Macrofauna F-statistic	Comparison of Treatments
A. *Gemma*		
exclusion × tube number	12.7**	Ca6 U0 U6 Ca0 (1246) (1025) (722) (640)
B. Total Polychaetes		
exclusion	48.6****	Ca > U (188.2) (37.2)
position	14.9***	In > Ou (171.6) (53.8)
tube number	5.8*	6 > 0 (151.4) (74.0)
position × tube number	10.1**	In6 In0 Ou0 Ou6 (128.6) (43.0) (31.0) (22.8)
C. *Polydora*		
exclusion	24.2****	Ca > U (76.3) (16.5)
position	21.6****	In > Ou (84.9) (7.9)
tube number	14.3***	6 > 0 (80.8) (12)
position × tube number	17.9***	In6 In0 Ou0 Ou6 (77.8) (7.7) (4.3) (3.6)
D. *Streblospio*		
exclusion	43.2****	Ca > U (38.3) (3.2)
position	5.9*	In > Ou (27.6) (13.9)
tube number	4.8*	0 > 6 (29.3) (12.2)
	II. Meiofauna	
A. Nematodes		
exclusion	12.4***	Ca > U (138.3) (95.0)
tube number	4.1*	6 > 0 (132.2) (101.4)
B. Total Copepods		
treatment	16.0****	Ca > U (72.1) (34.9)

Table 8. (Continued)

	I. Macrofauna F-statistic	Comparison of Treatments			
tube number	8.6**	6 > 0			
		(69.8)	(37.2)		
exclusion × tube number	9.1**	Ca6	Ca0	U0	U6
		(52.5)	(19.6)	(17.6)	(17.3)
C. *Leptastacus* sp.					
exclusion	27.6****	Ca > U			
		(41.5)	(13.9)		
tube number	10.5***	6 > 0			
		(37.4)	(18.2)		
position × tube number	4.5*	In6	Ou6	Ou0	In0
		(22.9)	(14.5)	(11.8)	(6.4)
exclusion × tube number	6.2*	Ca6	Ca0	U0	U6
		(30.4)	(11.3)	(7.0)	(6.9)
D. Juvenile *Gemma*					
exclusion	13.3***	Ca > U			
		(49.6)	(21.3)		

Diopatra tube density in the caging experiment. As shown in Table 8 the densities of *G. gemma* do not show a coherent tube density or treatment relationship although there is a significant treatment × tube number interaction. The pattern of interaction is not readily interpretable because densities of *G. gemma* in cages with 6D are greater than in cages with 0D (Table 8).

After 2 weeks polychaete densities were greater inside complete cages than in unmanipulated areas (Tables 3, 4, and 8) as had been reported by Woodin (1978, 1981) after much longer time periods (1974, 5 months; 1975, 2 months; 1976, 3 months). As expected for control sites, but not cage sites, inner areas with 6D had higher densities of polychaetes compared to 6D outer, 0D outer, and 0D inner areas in both cage and unmanipulated areas (Table 8). Thus after 2 weeks the densities increased inside of cages but the higher densities of polychaetes in 6D inner samples remained. As was evident in Woodin's data, the 6D refuge is imperfect in that densities from 6D sites inside cages were higher than from 6D unmanipulated sites (Table 3).

The patterns documented for total polychaetes were also noted for *Polydora ligni* (Tables 3 and 8), the most abundant polychaete found in 6D areas during our study (Table 2). Both Holland *et al.* (1980) and Virnstein (1979) have also reported increases in *Polydora ligni* densities inside cage exclosures in nearby Virginian sites. The other abundant species, *Streblospio benedicti,* increased inside of cages and inner areas after 2 weeks but displayed increased abundances in 0D versus 6D sites in both cages and unmanipulated treatments (Tables 3 and 8). The exact reason for this negative association with tube density is unknown although Woodin (1978) noted how

the relationship between tube density and *Streblospio benedicti* was temporally inconsistent over the years of her previous studies.

Densities of dominant meiofaunal taxa also increased inside cages after 2 weeks (Tables 3, 4, and 8). Given the lack of association with 6D tubes in inner control areas we did not expect to see a pattern related to tube density in the caging experiment. However, nematode densities were greater in 6D areas in cages and unmanipulated sites. In this case, the association with 6D was not localized to just inner areas but was evident in both inner and outer areas. Juvenile *Gemma gemma* had higher densities inside cages after 2 weeks (Tables 3, 4, and 8) but, unlike adult *G. gemma,* displayed no complex exclusion × tube number interaction (Table 8). Significant exclusion × tube number interactions were uncovered for total copepods and the dominant species, *Leptastacus* sp. (Tables 3, 4 and 8), with highest densities being found inside cages with 6D (Tables 3 and 4) compared to other treatment-tube number combinations. *Leptastacus* sp. also showed significant position × tube number interactions after 2 weeks with inner areas with 6D having much higher numbers of individuals than 0D inner or 6D or 0D outer areas (Tables 3, 4 and 8). Note however that this was true both inside cages and in unmanipulated sites. This latter pattern is similar to patterns uncovered for adult polychaetes for 2 weeks. In the latter case, aggregations around 6 tubes still persisted after 2 weeks inside cages.

e. Macrofauna and meiofauna: 4-week experiment. After 4 weeks, densities of *Gemma gemma* were significantly lower inside cages compared to unmanipulated sites (Tables 5, 6 and 9). Again, no readily interpretable association with tube number was uncovered. *G. gemma* densities in unmanipulated areas did not differ significantly in association with tube densities although *G. gemma* densities in cages with 3D or 6D were much higher than those with 0D and 1D (Tables 5, 6 and 9).

Polychaete densities, unlike *G. gemma,* were higher inside cages compared to unmanipulated sites after 4 weeks (Table 9) as was true after 2 weeks (Table 8). The patterns predicted to support the refuge hypothesis were not present during this time, however, as no interactions with tube number were discerned (Table 9). However, densities in unmanipulated 6D inner samples were still significantly greater than in other inner or outer unmanipulated sites (Table 5). It is this effect which should give the significant interaction in the ANOVA. Its absence may be due to the form of the significant exclusion × position interaction. Examination of exclusion × position interactions for polychaetes revealed that densities from cage outer areas were much greater than cage innner areas; the reason for this discrepancy is unknown. This inner-outer difference, however, did not appear in unmanipulated sites (Table 9).

Two polychaetes, *Heteromastus filiformis* and *Paraonis* sp., which were abundant in September 1980 samples (Table 2) increased in abundance inside cages, and showed no association with tube number or position (Tables 5, 6, 9) as we had predicted for the refuge hypothesis. Neither of these two species had been reported previously to

Table 9. ANOVA on I. macrofaunal and II. meiofaunal taxa from tables 5 and 6 from 4 week experiment. Means (in parentheses) are given below treatments. For those main effects which were identified as significant the direction of significant difference is indicated. Underlined treatments in Fisher significant difference test are not significantly different from one another ($P > 0.05$). The order of means (highest to lowest) is presented for those interactions which were identified as significant (no test of significance among interaction terms is possible). 0, 1, 3, 6 = tube number. Other abbreviations as in Table 8.

I. Macrofauna

	F-statistic	Comparison of treatments of Fisher significant difference test
A. *Gemma*		
exclusion	88.5***	U > Ca (5420) (1606)
exclusion × tube number	3.1*	U3 U6 U0 U1 Ca6 Ca3 Ca1 Ca0 (1475) (1347) (1326) (1272) (573) (542) (253) (238)
B. Total polychaetes		
exclusion	67.1****	Ca > U (551) (125.1)
exclusion × position	17.5****	Ca0 CaIn UIn U0u (362) (189) (76.5) (48.6)
C. *Heteromastus*		
exclusion	23.1****	Ca > U (144) (11.8)
D. *Streblospio*		
exclusion	94.6****	Ca > U (238.1) (26.2)
position	19.2****	Ou > In (186.6) (77.7)
tube number	4.2**	0 3 1 6 (97.6) (64.6) (57.1) (45.0)
exclusion × position	8.7**	CaOu CaIn UOu UIn (172) (66.1) (14.6) (11.6)
E. *Paraonis* sp.		
exclusion	4.4**	Ca > U (42) (16.8)

II. Meiofauna

A. Nematodes		
exclusion	37.1****	Ca > U (212) (111.3)
exclusion × tube number	6.4**	Ca6 Ca1 Ca0 Ca3 U0 U1 U3 U6 (62) (58) (53) (37) (30) (26) (25.3) (16)
B. Total Copepods		
exclusion	86.0****	Ca > U (172.6) (60.2)
position	29.1****	In > Ou (154) (78.8)
exclusion × position	6.0**	CaIn CaOu UIn UOu (120.5) (52.1) (33.5) (26.7)

Table 9. (Continued)

	I. Macrofauna				
	F-statistic	Comparison of treatments of Fisher significant difference test			
C. *Leptastacus* sp.					
exclusion	49.6****	Ca > U			
		(103.4) (31.8)			
position	21.8****	In > Ou			
		(92.3) (42.9)			
exclusion × position	7.4**	CaIn	Ca0u	UIn	U0u
		(75.1)	(28.3)	(17.2)	(14.6)
D. *Zausodes arenicolus*					
exclusion	49.4****	Ca > U			
		(30.1) (8.4)			
position	4.5**	In > 0u			
		(23) (15.5)			
E. Nauplii					
exclusion	36.8****	Ca > U			
		(23.3) (6.4)			
position	4.1**	In > Ou			
		(18.7) (11.0)			
F. Juvenile *Gemma*					
exclusion	22.6****	Ca > U			
		(81.3) (50.7)			
position	13.7****	In > 0u			
		(77.0) (55.0)			

increase in abundance inside cages (Woodin, 1981; see also Holland *et al.*, 1980; Virnstein, 1979). It has been suggested that adult *H. filiformis,* which is a subsurface deposit-feeder, has a refuge in depth (see above studies). Mortality of *H. filiformis* is a function of size and although adults may escape epibenthic predators, juveniles of *H. filiformis* may be extremely vulnerable to surface predation (Shaffer, 1983). Heavy predation on juvenile stages may explain the increases noted inside cages in this study. Unfortunately juveniles of *H. filiformis* were not sufficiently abundant to test this directly. Again, use of a small size (<0.5 mm) sieve may be critical to uncovering such a pattern. Also, only in one instance was either *H. filiformis* or *Paraonis* sp. abundant in the 1974–1976 samples (Table 2). Their failure to respond in earlier experiments may merely reflect the temporal variability of the assemblage's composition.

During September, *Streblospio benedicti* increased in density inside cages but displayed an inverse relationship between abundance and tube density. As in August, *S. benedicti* had highest densities in 0D sites (Table 9) and in cage outer areas while unmanipulated sites had similar densities in inner and outer locations. It is evident from inspection of density means and standard deviations of *S. benedicti,* as well as those of other polychaete species, that our predicted interactions may not have been discerned because of the large variability in single species abundance. Results for individual polychaete species should thus be interpreted cautiously.

All meiofaunal taxa increased in density inside cages compared to unmanipulated sites after 4 weeks (Tables 5, 6 and 9). A significant exclusion × tube number interaction was found for nematodes inside cages. Cage 6D had greater densities of nematodes than any other exclusion—tube number combination. Control 6D sites had very low numbers (Tables 5, 6, and 9). Total numbers of copepods and *Leptastacus* sp. increased inside cages after 4 weeks and increased more in inner areas than outer areas. Densities in areas from unmanipulated sites were similar to outer manipulated sites (Tables 5, 6 and 9) although this was not true for inner manipulated sites. Also, in contrast to the 2-week experiment (Table 8), no association with tube number was revealed. *Zausodes arenicolus* and nauplii of all species both showed higher densities inside cages in inner areas; this was true also in unmanipulated sites (Tables 5 and 9). The increase in juveniles of *Gemma gemma* inside cages cannot be separated from cage artifact (Table 7). Note however that densities inside cages were higher than unmanipulated sites in direct contrast to the lower densities of adult *G. gemma* inside cages during this time (Table 9).

Unfortunately, juvenile polychaetes were present in low densities in meiofaunal cores on all dates ($\bar{x}$ density 2-week control = 0.33; 2-week cage = 1.1; $\bar{x}$ density 4-week control = 0.25; 4-week cage = 0.77) and therefore were not subjected to statistical analyses. A number of trends are interesting, however. Most juveniles (>80%) were *Streblospio benedicti* while juveniles of *Heteromastus filiformis* and unidentified species composed the remaining 20% of young polychaetes. Mean densities of juvenile polychaetes were higher inside cages than noncaged sites after both 2 and 4 weeks which suggests that epibenthic activities may reduce numbers not only of adult cage classes of polychaetes but also juveniles. Densities of juveniles from inner and outer areas as well as a variety of tube densities were of similar magnitude. Also these results suggest that the effects of adult-larval or adult-juvenile interactions were weak in comparison to the predator/disturber effect. There was little evidence of aggregation of larvae around structure as predicted by the "larval accumulation" hypothesis (see also Eckman, 1983). Accumulation, however, that occurs initially at settlement or within days after settlement may be obscured by mortality or migrations of earliest stages.

f. Summary of caging results. A significant increase in total number of macrofaunal polychaetes was recorded inside predator/disturber exclusion cages after 2 and 4 weeks (Tables 8 and 9) which is consistent with previous reports (Woodin, 1981). Those species which were numerically abundant in control sites were also dominant inside cages (Table 2). Position × exclusion interactions for polychaete densities in the 4-week experiment were also uncovered with our analyses but these findings were not consistent with predictions for refuge utilization. Density levels of *Gemma gemma* were markedly higher than earlier studies (Table 1) and adult *G. gemma* displayed patterns strongly opposite to those of polychaetes (Tables 8 and 9), as had been

suggested by Woodin (1981). Tube number effects were also repeatedly uncovered for *G. gemma;* i.e., cages with 6D had a higher number of individuals than cages with 0D after the 2-week experiments and after 4-week densities of *G. gemma* did not decrease as greatly inside cages with 3D or 6D compared to 0D or 1D. The lack of significant differences between control sites, sides only, and tops only cage controls over 2 and 4 weeks as well as the order of densities from these treatments suggest that macrofauna responded to predator/disturber exclusion rather than cage structure (Table 7).

Dominant meiofaunal taxa also increased in density inside cages after 2 and 4 weeks (Tables 8 and 9). Significant exclusion × tube number and exclusion × position interactions were detected but no patterns corresponded to our *a priori* predictions for refuge utilization. As was true for the macrofauna, those meiofaunal species which were dominant in control areas were also dominant inside cages. Numbers of juvenile *Gemma gemma* increased inside cages unlike adult *G. gemma* which decreased in density inside cages relative to controls after 4 weeks. The increase in densities of juvenile *G. gemma* may be related to exclusion of predators/disturbers or some cage artifact (Table 7). Cage effects were not discerned for other meiofaunal taxa.

4. Discussion

This study examined community unity of two, operationally-defined size classes of soft-bottom fauna by investigating the nature and temporal aspects of responses of both macrofauna and meiofauna to manipulation of epibenthic predators/disturbers. Concurrently, similarity in utilization of biogenic structural refugia by both size classes was investigated. In the experiments presented above both macrofauna and meiofauna increased in density inside predator/disturber exclusion cages, and this response was evidenced on the same time scale; i.e., 2–4 weeks (Tables 8 and 9). In many cases the increase in abundance inside cages was dramatic. This increase even in 6D sites further demonstrates that the tubes are not complete refuges. The one exception was by adult *Gemma gemma* which decreased inside cages after 4 weeks (Tables 5, 6, and 9). Only juvenile *G. gemma* exhibited possible cage artifacts at the termination of the 4-week experiment (Table 7). No cage artifact was detected during the 2-week experiment (Table 7). Along with the density increases noted inside cages a variety of main effects (tube number or position) and interactions were revealed. These tube number and position effects and interactions were not consistent even among taxa of the same size class. Thus, although densities of both meiofauna and some macrofauna increased over similar time scales in response to predator/disturber exclusion, their spatial patterns and relationships with tubes were highly variable (Tables 3, 4, 5, 6, 8 and 9). The exact reasons for the differences in spatial patterns among the benthos were not scrutinized here and remain unknown; our results, however, clearly point out that the spatial patterns are not consistent with predictions of aggregations around tubes for all taxa.

Our sampling of two benthic size classes provides comparisons of patterns of

abundance of different age classes of *Gemma gemma*. Note that second order interactions for juvenile bivalves are not the same as those for their adult counterparts (Tables 8 and 9). Moreover high densities of juvenile *G. gemma*, but not adults, are found inside sides only cage controls (Table 7). Our findings are somewhat analogous to those of Buzas (1978) who found no integration of responses of macrofaunal-size molluscs and meiofaunal-size taxa (foraminifera). These results reaffirm that processes controlling the abundance of these age/size groups may be distinct.

Other manipulative studies using a 1 mm sieve have not reported a significant effect of predator exclusion on *Gemma gemma* densities (Woodin, 1978, 1981; Wiltse, 1980) although Woodin (1981) did find an increase in *G. gemma* densities in areas where only *Limulus polyphemus* was excluded from April to July 1976 [see also Green and Hobson (1970)]. Therefore the increase (Table 3) and subsequent drastic decrease (Table 5) in *G. gemma* density inside cages in our experiments are unique. Note, however, that other bivalves may show evidence of predator regulation [e.g., *Mulinia lateralis* (Virnstein, 1977)]. The marked decrease in *G. gemma* was not discerned for the juvenile age class as densities of juvenile *G. gemma* were repeatedly greater inside cages versus controls (Tables 3, 5, 8 and 9). The differences were significant only at 2 weeks. The increase charted inside cages for juvenile *G. gemma* is consistent with Sellmer's (1967) report of high mortality due to predation by epifauna at early ages. Woodin (1981) suggested that cage structure may interfere with feeding by *G. gemma* and increase the emigration rate thereby causing the observed decreased *G. gemma* densities. Similar migratory behavior was invoked by Peterson and Andre (1980) to explain the absence of the bivalve, *Saxidomus*, in areas of high densities of other suspension feeders which compete for space. Whether the decreases in densities of adults noted after 4 weeks are due to interference with feeding or interactions with other organisms cannot be determined from our study. Woodin (1981; p. 1064) also suggested that the lack of increase in *G. gemma* density in cages found in previous studies was due to interactions with increased polychaete numbers which mask any response to predator exclusion. In experiments reported here, however, polychaete densities did not increase substantially inside cages after 4 weeks compared to 2 weeks while *G. gemma* densities did change dramatically (Tables 5 and 6), thereby lending little credence to the previous interference proposal. Finally, the results charted for *G. gemma* over the 4 weeks of our experiment are even more perplexing because adult *G. gemma* consistently displayed a significant relationship with tube densities inside cages (Tables 8 and 9). Inspection of these data suggests that high densities of *G. gemma* are associated with higher tube densities (Tables 3 and 5). Such an association with tubes was unexpected [see Woodin (1978) and (1981)] and remains unexplained.

The polychaetes with more than an average of five individuals in any treatment were analyzed separately. Only one, *Polydora ligni*, showed significantly higher densities around 6 *Diopatra* tubes (Tables 8 and 9). The other spionid, *Streblospio benedicti*, showed higher densities with 0 *Diopatra* tubes. Woodin (1978) had previously reported that the association of *Streblospio* with *Diopatra* tubes was temporally variable.

Polydora is known to inhabit the surfaces of the tube-cap of *Diopatra* (Bell and Coen, 1982; Bell unpubl.) as well as the surrounding sediment which may account for some of the difference in responses of these two spionids. The increase in *Polydora ligni* noticed in high tube densities, therefore, may be due to an increase in densities within sediments surrounding *Diopatra* or an increase in *P. ligni on* tube-caps. Contamination of *P. ligni* from tube-caps should be minimized, however, because tube-caps were removed prior to sediment sampling.

Few previous reports on predation/disturbance effects and the meiofaunal taxa examined here exist although the copepod species are widely distributed along the eastern coast of North America. In the northern Gulf of Mexico, Reidenauer and Thistle (1981) showed that *Zausodes arenicolus* was completely removed from areas disturbed by stingrays. Increases in meiofaunal taxa in predator-disturber manipulative experiments have been reported in other experiments in a salt marsh in South Carolina (Bell, 1980) and in mudflats in the North Sea (Reise, 1979). In the former study copepod and juvenile polychaetes increased seasonally inside cages over the time scale of weeks while nematodes increased only rarely (Bell, 1980). Reise (1979) found an increase in juvenile macrofauna and nematodes inside cages over 64 d but noted no change in copepod densities. Fleeger *et al.* (1981) and Berge (1980) found no difference in meiofaunal densities in predator exclusion cages versus controls after 2 and 7 months, respectively. In our experiments both nematodes and copepods displayed an increase in density inside predator exclusion cages compared to control sites (2 wk: Tables 3, 4, and 8; 4 wk: Tables 5, 6 and 9). Our experiments were not run long enough to determine whether the high densities of meiofaunal taxa recorded inside cages would return to control levels as repeatedly found in Bell's (1980) experiments in the salt marsh.

As mentioned above, the time scale used in this experiment was deliberately chosen as a compromise between expected meiofaunal and macrofaunal response times. Although our experiments were somewhat shorter than Woodin's 2 and 3 month experiments (1974–1974) our results from caging experiments are comparable. In 1974 and 1975 Woodin documented an order of magnitude increase in total polychaetes inside predator exclusion cages after two months. Such an increase was seen here for total adult polychaetes in 6D sites after two weeks (Table 3) and for *Heteromastus filiformis* and *Streblospio benedicti* in some sites as well as the dominant meiofaunal copepod, *Leptastacus* sp. in 6D sites after 4 weeks (Table 5). Thus the experimental period was long enough to see responses by members of both the meiofauna and macrofauna. Given the goals of our study as outlined previously and our documented results, the short term experiments appear both necessary and sufficient for our experimental purposes.

Although we found consistent increases in densities inside cages for both macrofaunal and meiofaunal taxa which suggest that predation/disturbance influences abundance of these benthic groups (Tables 8 and 9), statistical analyses of spatial patterns

only partly support our predictions for a "refuge" hypothesis (see Methods and Materials). During the course of these experiments, as Woodin (1978) had observed for total polychaetes during August 1974 (Table 2), many taxa did not show the expected pattern of increased abundances around 6D inner areas. When we took samples initially in April 1980 to confirm the presence of a refuge effect for the meiofauna, such an effect was seen at least for copepods in unmanipulated areas: inner samples: [6D:15(±6.5); 0D: 7.1(±3.2)]. In August 1980 however the only group which showed a consistent refuge effect in unmanipulated areas was the polychaetes (Table 8), the group for which Woodin (1978, 1981) had previously demonstrated this effect. This was true of polychaete densities in September 1980 as well (inner: 6D:30.4(9.0) 0D: 12.5(6.2), $F = 26.5$, $0.01 \leq P < 0.05$). Note however that contrary to our expectation this effect was not evident in the results of the three-way ANOVA. Depending on the speed of the response of the polychaetes, we expected one or more of the following terms to be significant: tube number (6D > 0D), position × tube number (inner 6D > inner 0D = outer 6D = outer 0D), position × exclusion × tube number (cage 6D = cage 0D > inner unmanipulated 6D > inner unmanipulated 0D = outer unmanipulated 6D = outer unmanipulated 0D). If the polychaetes responded to the manipulation within the time course of the experiment (2 or 4 weeks), then the tube effect seen in unmanipulated areas should be revealed as a significant position × exclusion × tube number effect. If the polychaetes had either not yet responded or had not responded to the extent of masking the original 6D versus 0D contrast, then we expected a significant tube effect and a significant position × tube number interaction term. In August, after two weeks, this was true (Table 8). Both tube number and position × tube number were significant. In September, after 4 weeks, it was not true (Table 9). None of the terms we expected to be significant were, although the control samples still showed a significant effect associated with tube number (Table 5).

None of the remaining taxa showed significant effects associated with tube number in unmanipulated areas analyzed separately in August or September. Several of these taxa did, however, show significant tube number effects in the three way ANOVA (Table 8; nematodes, total copepods, *Leptastacus,* after 2 weeks). None showed such effects after 4 weeks (Table 9) and none showed the expected significant exclusion × position × tube number interaction.

Other disparities between the results found here and earlier investigations are worthy of mention. The polychaete species reported to increase inside cages and demonstrate a refuge effect in previous experiments, *Spiochaetopterus, Nereis,* and *Tharyx,* were not common in our study period indicating between year variability in community composition (see also Table 2) as also noted by Woodin (1981). Variability of a shorter term was recorded for meiofauna as well: in April we charted localized increases in copepods around 6D in unmanipulated areas which suggested the presence of a refuge effect for meiofauna taxa. In the fall no such localized increases were observed for meiofauna taxa and thus patterns predicted to support a refuge hypothesis

were not discerned. The 4 dominant harpacticoid copepods *Leptastacus* sp., *Zausodes arenicolus,* Diosaccid sp. and *Paralaophonte* sp. were present both in April and August so that differences in distributional patterns do not appear to be related to variation in species composition as was true for some polychaetes. The lack of aggregation by meiofauna taxa, including juvenile *Gemma gemma,* may be a result of constant reshuffling of species distributions over very short time scales (tidal cycles; days) in the sand flat especially in response to newly disturbed sediment patches (Thistle, 1981). The bulldozing effect of *Limulus* which is apparent in summer months only may act to increase sediment and meiofaunal movement (e.g., Bell and Sherman, 1980; Palmer and Brandt, 1981) thus negating any localized increases in density around tubes as was common in April. Differences in microfloral and microfaunal components of the sediments may also be responsible for the seasonal differences in distributional patterns.

The above discussion suggests that much of the discrepancy between the findings of this study and earlier reports of macrofaunal utilization of *Diopatra* tube-caps as refuges (Woodin 1978; 1981) may be related to changes in community composition (Table 2), predator activity, or the time scale of our experiments (2 to 4 wks vs. 2 to 6 mos). It is curious that we did not obtain similar results for all taxa from experiments conducted in a previously well-studied system. It is interesting, however, that we did document the refuge pattern for total polychaetes (but different species) in August 1980 as Woodin (1978; 1981) had repeatedly demonstrated. Questions which emerge from our study are (1) how consistent are population levels and community composition over the time scale of years in a given area (e.g., Table 2), (2) how repeatable are field experiments in soft-bottom habitats over similar time intervals [but see Woodin 1981)], (3) how long must such field experiments run and (4) precisely why do we see similarities or differences in 1–3 above for different size classes of benthos? Because much information on forces organizing soft-sediment communities has been inferred from field experiments and short-term monitoring of communities, it is instructive to know how variable results might be over ecological time. To our knowledge, no study has critically evaluated these questions.

Results from coincident investigations of both macrofaunal and meiofaunal benthos are of broad interest in understanding processes which inherently structure benthic communities. Because size class interactions between macrofauna and meiofauna, such as competition between juvenile macrofauna and permanent meiofauna, predation by meiofauna on settling macrofaunal larvae, or mortality of meiofauna caused by sediment processing of infauna (see Bell and Coull, 1980) have been documented, these size classes are linked within the community infrastructure (*sensu* Paine, 1980). Thus alteration of predator/disturber activities may have implications for community composition. Moreover, delineation of patterns of response and temporal aspects of response by both macrofauna and meiofauna to disturbed patches may be critical for describing successional processes if size class interactions are also mechanisms responsible for facilitating or inhibiting community change.

Much of the aforementioned commentary has focused on two size classes within the benthos. Certainly a more complete approach to studying community dynamics in sediments would include microbiota also, given that microbial relationships with macrofauna and meiofauna are of interest (e.g., Gerlach, 1978; Levinton *et al.*, 1977; Lopez *et al.*, 1977; Reiper, 1978; Tietjen, 1980). Although such an approach is logistically problematic, it may well be necessary for developing ecologically sophisticated insight into size class interactions and ultimately organization of soft-bottom communities.

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